

HERITABILITY ESTIMATES AND INBREEDING
EFFECTS FOR SELECTED AGRONOMIC
CHARACTERS IN EASTERN GAMAGRASS,
TRIPSACUM DACTYLOIDES L.

By

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CHAPTER I

INTRODUCTION

Oklahoma is one of the leading states in the USA in beef cattle production. The availability of inexpensive, high-quality forage would contribute to the success of that beef industry by providing higher animal gains while reducing the amount of land area required for production. Quality forage would also substitute, in part, for the feed grain concentrates required in the "finishing" process of livestock. However, late spring through summer is a period in the Oklahoma "forage calendar" that is deficient in high-quality forage. Neither the perennial, warm-season native or introduced species currently used by producers maintain high forage quality throughout the summer months.

Eastern gamagrass (Tripsacum dactyloides L.) is a warm-season perennial species which may prove to be an asset to forage producers in Oklahoma. This species has a reputation among cattlemen as a highly productive and palatable plant, but very little research has been conducted to verify those claims. As part of a continuing series of studies on eastern gamagrass at Oklahoma State University, this investigation was undertaken to determine the amount of heritable variation and inbreeding effects for selected

agronomic characters in eastern gamagrass.

The breeding method used for a given species depends on the rate of character response to selection, the mode of pollination, and the type of cultivar to be produced. The level of improvement expected from selection depends on the amount of heritable variation (i.e. that which is transmitted to progeny) rather than environmental variation (that which is peculiar to a single set of climatic and cultural circumstances). Chapter II describes the work completed on the determination of heritable variation for plant weight, seed weight, fertility, percent in vitro dry matter digestibility, and percent crude protein. The potential for improving these respective traits in eastern gamagrass using individual, half-sib family, and progeny test selection is explored.

Eastern gamagrass normally reproduces by cross-fertilization; therefore, natural populations are highly heterogeneous and heterozygous. Inbreeding in normally cross-fertilized species usually results in a decrease in plant vigor and fertility. Chapter III contains the results of a study concerning the effects of inbreeding on plant height, plant weight, seed weight, and fertility in eastern gamagrass. Information of this nature helps determine how large a breeding population must be to avoid inbreeding depression and whether selfing can be utilized as a tool for selecting superior individuals.

The manuscript was written in the style acceptable to

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CHAPTER II

HERITABILITY ESTIMATES FOR SELECTED AGRONOMIC CHARACTERS IN EASTERN GAMAGRASS

Abstract

A 2-year field study was conducted on eastern gamagrass (*Tripsacum dactyloides* L.) to determine narrow-sense heritability estimates on a half-sib (HS) family and individual plant basis for plant weight (PW), 100-seed weight (SW), percent of florets setting pure live seed (PLS), percent in vitro dry matter disappearance (IVDMD), and percent crude protein (CP). The material included 75 parental clones and their 50 F_1 offspring populations. The parents were a random sample selected from a space-planted nursery of open-pollinated offspring produced by a heterogeneous, heterozygous composite population. This source population was an advanced generation of the original composite of a large number of accessions collected from throughout the southern Great Plains. Parental clones and F_1 offspring were arranged in a randomized complete block design with four replications. An unweighted means analyses of variance and covariance was computed for male parents and their HS offspring.

The means, ranges, and error coefficients of variation

(CV) for all characters were similar between parents and their respective offspring. The genetic CV's were all higher for the parents than for offspring. The genetic variation among parents and HS families was significant for all characters, except PLS in HS families. A significant genotype by year interaction occurred among HS families for PW and among parents for PLS. Variance component estimates of narrow-sense heritability computed on a HS family mean basis (H_f) were higher than estimates on an individual plant basis (H_i). The H_f and H_i estimates were high for SW, medium to high for IVDMD and CP, low for PW, and very low for PLS. Estimates of heritability computed on a plot-mean basis using parent-offspring regression (H_{po}) were lower than H_f estimates, except for 100-seed weight. Predicted genetic gains indicate that individual plant selection would be the most effective means for improving PW, SW, IVDMD, and CP. Predicted response for PLS was greatest for selection of parental clones based on performance of their HS progeny.

Additional index words: Tripsacum dactyloides L., Genetic variation, Narrow-sense heritability, Plant weight, Seed weight, Pure live seed, Forage quality, Near infrared reflectance.

Introduction

The genus *Tripsacum* is a member of the tribe Maydeae along with maize (*Zea mays* L.) and teosinte [*Zea mays* spp. *mexicana* (Schrader.) Iltis]. Eastern gamagrass (*Tripsacum dactyloides* L.) is a perennial, warm-season, tall-growing bunchgrass native to the eastern USA. The species is normally found on alluvial bottomland soils with favorable moisture conditions (5, 9). Individual plants may reach a height of 3 m and have a crown diameter of 1.5 m (6, 11). Eastern gamagrass (gamagrass) produces several tillers during the growing season (5). Terminal inflorescences may have one to ten racemes while axillary inflorescences usually contain a single spike. The racemes of the inflorescence have staminate spikelets on the upper portion and pistillate spikelets on the lower portion (6). The species is protogynous and normally cross-pollinated; however, self-fertilization does occur because of the absence of self-incompatibility.

Gamagrass has a reputation as a highly palatable and productive species. It has almost been eliminated from range sites where it once flourished because of its erect growth habit and livestock grazing preference (1). Despite its perceived forage yield and quality potential, gamagrass is not extensively grown because of inadequate seed production, inferior seed quality, difficulties in vegetative establishment, and lack of persistence under grazing (1, 11, 14). However, Ahring and Frank (1)

demonstrated that good stands of gamagrass could be established if high quality seed were planted.

Gamagrass expresses a considerable amount of phenotypic variation (9, 14). Newell and de Wet (9) found 235 eastern gamagrass accessions, collected from 10 states, to be highly variable morphologically and composed of populations with distinctive character combinations. Diploid gamagrass ($2n = 2x = 36$) predominated in the Great Plains region, and tetraploid gamagrass ($2n = 4x = 72$) was more common in the eastern United States. However, no single morphological characteristic distinguished diploids from tetraploids.

Wright et al. (14) reported that the initiation of flowering of 51 gamagrass accessions collected from throughout Texas and Oklahoma extended from early May to the middle of June. Percent seed set ($\bar{x} = 55\%$, range 10 to 90%) appeared to be linked with meiotic stability. Diploids had greater meiotic stability and higher percent seed set values than accessions having more than 36 chromosomes. The mean IVDMD of the 51 accessions sampled during May ($\bar{x} = 67\%$), June (62%), and July (53%) decreased with advancing maturity in a nearly linear manner. Forage quality was more stable in some accessions than in others as indicated by a significant accession by sampling date interaction. Significant phenotypic variation was also present for spring growth vigor, anthesis date, and regrowth vigor.

To develop an effective and efficient breeding program for improving gamagrass, more information about the

heritable variation present for agronomic characters would be useful. Therefore, this study was undertaken to determine narrow-sense heritability estimates for selected agronomic characters and to use this information to ascertain the potential genetic gain for those characters.

Materials and Methods

The plant material used in this study consisted of 75 gamagrass parents and 50 F_1 offspring populations. The parental plants were randomly selected from a nursery of space-planted, open-pollinated offspring from a large genetic base population. This population traces to a composite population of a large number of gamagrass accessions collected from throughout Kansas, Oklahoma, and Texas. This highly heterogeneous, heterozygous source population was maintained at the Southwestern Livestock and Forage Research Station, El Reno, Okla.

The 75 parents were randomly grouped into sets of three, in which two plants were then randomly designated as female parents. F_1 progeny were produced for each of the 25 sets by mating the male parent to each of the two females. In January 1976, the F_1 seed were cold stratified in plastic germination trays at 10°C for 4 weeks as suggested by Ahring and Frank (1). Trays were then transferred to a germination chamber; and soon after germination, seedlings were transplanted into small pots in the greenhouse. Each of the parents was increased at this time by vegetative

propagules.

In May 1976, the parental clones and F_1 offspring were planted in a randomized complete block design with four replications. Each plot contained 10 parental clones or 10 F_1 seedlings planted 1.2 m apart. The experiment was located at the Agronomy Research Station, Perkins, Okla. In early March 1982 and 1983, the plots were burned, and a pre-emergence herbicide was applied for weed control. The soil was a Teller loam (Udic Arguistoll), and the study was fertilized each spring with 80 kg N/ha.

The traits evaluated in 1982 and 1983 were plant weight (PW) adjusted for moisture, 100-seed weight (SW), and fertility. Forage quality was determined for plants harvested in 1982 only. Those variables included percent in vitro dry matter disappearance (IVDMD) and percent crude protein (CP).

PW was determined for two plants sampled at random from each plot during the first week of June in both 1982 and 1983. In a few of the parent and offspring plots only one plant was available for sampling. Each individual plant was tied at the center and then harvested 20 cm above the crown. A green forage sample was taken from each plant when harvested. Each green sample was dried in a forced-air oven at 45°C for 1 week and then weighed for determination of moisture percentage. PW was adjusted for moisture by multiplying each value recorded in the field by its respective moisture percentage.

In 1982, IVDMD and CP were determined for each dried sample. The forage samples were first ground through a 5 mm screen using a Wiley Mill¹. The ground forage was then separated into two equal subsamples, and one of those was reground through a 1 mm screen using a UDY Cyclone Mill¹. This sample preparation resulted in 20 to 30 g of ground forage which was used to determine forage quality.

IVDMD and CP were determined by near infrared reflectance (NIR) spectroscopy using a Neotec Model 6100 monochromator¹. The reflected energy (R) from sixty-four scans of each sample with monochromatic light in the near infrared region (i.e., from 1,100 to 2,500 nm) were averaged for each 2 nm increment and stored on a Digital Equipment Corp. mini-computer PDP 11L-03¹.

The monochromator was calibrated with IVDMD and CP data from laboratory analysis of 200 forage samples (10% of the total number of samples) selected at random from the entire experiment. Percent IVDMD for the laboratory analysis was determined in three replications using a modified Tilley and Terry technique (8). Percent CP was determined in two replications using the standard AOAC macro-Kjeldahl procedure (2). Calibration of the monochromator was achieved using computer software developed at Pennsylvania State Univ. (12). The software combined NIR reflectance data

¹ Mention of a trademark or proprietary product does not constitute a guarantee or warranty by the USDA or by Oklahoma State University and does not imply approval to the exclusion of other similar products.

with the laboratory analysis, performed the necessary mathematical transformations of the reflectance spectra ($\log 1/R$, first and second derivatives), and used a modified stepwise linear regression procedure to find the wavelengths most useful for predicting the desired forage quality trait. On the basis of the R-square, bias, and standard error of prediction statistics, an equation was chosen to predict the IVDMD and CP from the reflectance spectra of the remaining samples.

Seed heads were harvested during July 1982 and August 1983 for determination of SW and fertility. Fifteen to 20 seed heads were collected from each of two plants in each plot, excluding those previously harvested for PW. The heads were threshed by hand, and 50 seed units were counted out and weighed. A seed unit consists of hardened exterior glumes potentially enclosing a single caryopsis. Fertility was estimated by measuring the percent pure live seed (PLS) in each 50-seed unit sample as indicated by seedling emergence. Ten seed samples/flat (containing vermiculite) were planted in a greenhouse during November of both years. Seedling counts were started 3 weeks later, and continued at 2-week intervals until a total of 6 counts had been taken. The PLS percentages in 1982 were very low and may have resulted from harvesting immature seed (even though the harvest date was in late July). Because of the low PLS in 1982, seed heads were harvested a month later in 1983 (i.e., at the end of August).

Analyses of variance and covariance were computed on the unweighted plot means of male parents and HS offspring. A split-plot in time design was used as the model for characters on which 2 years of data were available (10, 13). Expected mean squares and cross-products were determined assuming a random effects model for replications, years, and parents (or HS families). The components of variance and covariance were calculated from linear functions of the mean squares or cross-products.

Narrow-sense heritability estimates were calculated on a HS family mean basis (H_f) and individual plant basis (H_i) since field and laboratory measurements were recorded on individual plants (7, 10, 13). The narrow-sense heritability estimates, H_f , were computed as the ratio of the genetic component of variance among HS families (s_{Go}^2) to the phenotypic variance of the offspring mean over replications, years, and plants within plots (Equation 1, Table 1). The H_i estimates were computed as the ratio of 4 times s_{Go}^2 to the phenotypic variance among individual offspring (Equation 2, Table 1). Narrow-sense heritability was also estimated using parent-offspring regression (H_{po}). The estimates of H_{po} were calculated as twice the ratio of the genetic covariance between parents and offspring (Cov_{Gpo}) to the phenotypic variance of the parent mean over replications, years, and plants within plots (Equation 3, Table 1) (4, 10).

Expected genetic gains were estimated for 1) mass selection (G_1) based on individual performance of F_1

offspring; 2) HS family selection (G_f) based on the phenotypic mean of HS families averaged over replications, years, and plants within a plot; and 3) parental clone selection (G_p) based on the phenotypic means of their HS progeny averaged over replications, years, and plants within a plot (Equations 4, 5, and 6, respectively; Table 1). All three selection methods assumed that the superior genotypes were isolated to control pollination during recombination (i.e., polycross) for the next generation. The first two selection methods would require at least 2 years/cycle, and the last method would require a minimum of 3 years/cycle. The expected genetic response for each selection method was expressed as a percentage of the mean and adjusted for the time to complete a cycle of selection.

Results and Discussion

The means, ranges, and error coefficients of variation (CV) for all agronomic characters studied were similar in magnitude for the parents and offspring (Table 2). Years were a source of significant ($P \leq 0.01$) variation for the characters studied in the parents and offspring. Year differences probably occurred because of precipitation differences for the 2 years. Fifty-one and 35 cm of precipitation were recorded for the first half of 1982 and 1983, respectively. The precipitation for May, 1982 was 24 cm above the long-term average.

Significant ($P \leq 0.05$) genotype by year interactions

occurred for PW and PLS among the HS offspring and parents, respectively. The mean PW for the offspring in 1982 (\bar{x} = 1.0 kg, range = 0.4 to 1.7 kg) was significantly ($P \leq 0.01$) greater than in 1983 (\bar{x} = 0.7, range = 0.01 to 1.6 kg). The mean PLS for the parents in 1982 (\bar{x} = 6%, range = 0 to 36%) was significantly lower than the estimate for 1983 (\bar{x} = 51%, range = 16 to 86%). The differences between means and ranges for the 2 years were also similar in magnitude for PLS in the offspring. In other studies seed set ranged from 10 to 90% and germination of pure-seed fractions ranged between 72 and 95% (1, 14).

The genetic CV's were higher for the parents than for HS offspring for all characters evaluated (Table 2). The only genetic CV greater than its corresponding error CV was that for SW, and it provides evidence for potential genetic improvement in that trait. Estimates of genetic variance components were always larger for the parents (s_{Gp}^2) than for the HS families (s_{Go}^2) or the covariance among parents and HS offspring (Cov_{Gpo}) (Table 3). These results were expected because the parents were clonal material; and therefore, the estimate of s_{Gp}^2 can be attributed to the total genetic variance present in the reference population (10). The genetic variance component arising from among HS families, s_{Go}^2 , was equal to the covariance among HS offspring and estimates one-fourth of the additive portion of the total genetic variance. The parent-offspring covariance (Cov_{Gpo}) estimates one-half of the additive

genetic variance present for a trait.

The estimates of s^2_{Gp} were significant ($P \leq 0.05$) for all agronomic characters studied (Table 3). Estimates of s^2_{Go} for HS families were also significant ($P \leq 0.05$) for all characters studied except PLS (which was significant at $P < 0.10$). The estimates of s^2_{Go} indicate that additive genetic variance accounted for a significant portion of the total genetic variance. The estimate of Cov_{Gpo} was negative for PW; but it was similar in magnitude to s^2_{Go} for SW, IVDMD, and CP. Theoretically, the value for Cov_{Gpo} should be twice the value of s^2_{Go} since those values estimate one-half and one-fourth of the additive genetic variance, respectively. The estimate of Cov_{Gpo} for PLS was much larger than s^2_{Go} .

Variance component estimates of narrow-sense heritability computed on a HS family mean (H_f) basis were higher than estimates computed on an individual plant (H_i) basis (Table 4). This result was expected because the H_f estimate is computed using variance components averaged over replications, years, and plants within plots. Both the H_f and H_i estimates indicate substantial improvement potential for SW, but the estimates for PW and PLS were very low. The two forage quality characters, IVDMD and CP, had high H_f and medium H_i values. However, these estimates may be biased upwards by genotype by environment interaction because they were based on only 1 year's data.

The H_{po} were lower than those estimated using variance

components for PW, higher for SW and PLS, and intermediate for IVDMD and CP. The estimates H_f and H_{po} for PLS based on 2 years data may be incorrect. The variance among HS families was significant ($P \leq 0.05$) in 1983 only. The estimates of H_f and H_{po} in 1983 were similar (37 and 45%, respectively) and indicate that the low estimates, using both years data, may be due to the problems with immature seed in 1982.

The H_i estimates for SW, IVDMD, and CP were sufficiently high to enable significant progress using individual plant selection (G_i) (Table 5). Even though the H_f and H_{po} estimates for these characters were higher than corresponding H_i estimates, the larger phenotypic standard deviations for individual plants (1.36 g, 2.65% and 0.81%, for SW, IVDMD, and CP, respectively) resulted in greater expected genetic gains. If evaluation of large populations were not feasible or the estimate of H_i was low, or both, then HS family selection could be used. However, SW is estimated easily; and the use of NIR allowed for rapid and precise determination of forage quality. Consequently, for these characters the screening of large populations is feasible and the breeder could take advantage of the larger phenotypic variation (that would be reduced if HS family selection were used).

The low H_i estimates for PW and PLS resulted in low G_i values (Table 5) even though phenotypic standard deviations among individual plants were high for both traits (0.24 kg

and 12.5%, respectively). HS family selection for PW and PLS had no apparent advantage over individual plant selection, but harvesting an entire progeny row could be more efficient than harvesting individual plants. However, Burton (3) suggested that with little training, one could visually estimate yields of Pensacola bahiagrass (Paspalum notatum var. saure 'Parodi') plants with a high degree of accuracy. If the three to four highest yielding gamagrass plants could be selected visually using some sort of grid system (5), then the labor involved would be greatly reduced and individual plant selection might be feasible.

The G_p estimate for PLS was substantially higher than the G_i and G_f estimates (Table 5), but the time required for completing a cycle of selection would require 3 to 4 years if selection of parental plants was based on offspring performance. Selection for PLS could be deferred until after selection for the other characters. A record of PLS for each of the selected genotypes which were combined under isolation could be used to decide if the progeny from these polycrossed parents should be advanced to the next space-planted nursery. Moreover, if equal numbers of offspring from the recombined parents were used, a larger effective population size would result. This method would reduce inbreeding depression since progeny from a single genotype would not occur at an unusually high frequency.

In summary, significant ($P \leq 0.05$) heritable variation occurred for all characters studied except for PLS.

However, the low estimates of additive genetic variance for PLS might have resulted because immature seed were collected during the first year. Selection of individual superior genotypes, and recombination of these genotypes in a polycross nursery would result in substantial genetic gains for all characters except PLS. Predicted responses indicate that greatest gains in PLS would result if parental clones were selected based on performance of their HS progeny.

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Table 1. Equations used to estimate narrow-sense heritability and expected genetic gains from selection.

Equation number	Parameter estimated	Equation†
1	Heritability on a mean basis for half-sib offspring for 2 years	$H_f = s_{Go}^2 / [s_{Go}^2 + (s_{GYo}^2/y) + (s_m^2/r) + (s_e^2/ry) + s_{w/ryn}^2]$
2	Heritability on an individual plant basis 2 years	$H_i = 4s_{Go}^2 / [s_{Go}^2 + s_{GYo}^2 + s_m^2 + s_e^2 + s_w^2]$
3	Heritability estimated by parent-offspring regression for 2 years	$H_{po} = 2s_{Gpo}^2 / [s_{Gp}^2 + (s_{GYP}^2/y) + (s_m^2/r) + (s_e^2/ry) + s_{w/ryn}^2]$
4	Gain from selection of individual plants	$G_i = (k/2)H_i[s_{Go}^2 + s_{GYo}^2 + s_m^2 + s_e^2 + s_w^2]^{1/2}$
5	Gain from selection of half-sib families	$G_f = (k/2)H_f[s_{Go}^2 + (s_{GYo}^2/y) + (s_m^2/r) + (s_e^2/ry) + s_{w/ryn}^2]^{1/2}$
6	Gain from progeny test selection	$G_p = (2k/3)H_{po}[s_{Gp}^2 + (s_{GYP}^2/y) + (s_m^2/r) + (s_e^2/ry) + s_{w/ryn}^2]^{1/2}$

† s_{Go}^2, s_{Gp}^2 = genetic variance components due to HS families and parents, respectively.

s_{GYo}^2, s_{GYP}^2 = variance components due to HS families (or parents) by year interaction, respectively.

s_m^2, s_{mp}^2 = variance components due to HS families (or parents) by replications interaction, respectively.

s_e^2, s_w^2 = experimental errors among plots and among plants within plots for HS families (or parents), respectively.

Cov_{Gpo} = genetic covariance between parents and offspring.

y, r, n = number of years, replications, and plants within a plot, respectively.

k = selection intensity (estimated at 10% level herein).

Table 2. Means, ranges, and coefficients of variation for selected agronomic characters in eastern gamma-grass parents (p) and half-sib offspring (o).

Character	Geno- type	Mean \pm SE†	Range	Error CV‡	Gene- tic CV
2-year estimates					
Plant weight, kg/plant	p	0.87 \pm 0.01	0.12 - 1.74	14.9	11.6
	o	0.85 \pm 0.01	0.07 - 1.79	10.5	3.5
100-Seed weight, g	p	8.1 \pm 0.06	4.8 - 12.2	6.7	10.9
	o	8.0 \pm 0.05	4.1 - 12.3	6.6	6.9
Pure live seed, %	p	29 \pm 1	0 - 86	23.5	13.5
	o	28 \pm 1	0 - 96	24.1	2.7
1-year estimates					
IVDMD, %	p	56.2 \pm 0.2	47.6 - 66.2	3.2	2.8
	o	56.6 \pm 0.2	46.8 - 66.2	2.7	1.4
Crude protein, %	p	9.1 \pm 0.1	6.3 - 11.2	6.5	3.8
	o	9.0 \pm 0.04	7.0 - 12.2	4.2	2.8

† Standard error of the mean.

‡ Coefficient of variation, %.

Table 3. Components of variance and covariance estimates for selected agronomic characters in eastern gamagrass parents (p) and half-sib offspring (o).

Character	Geno- type	$s^2_{G\#}$	s^2_m	s^2_{GY}	$s^2_e + (s^2_w/n)$
2-year estimates					
Plant weight, kg	p	0.011**	-0.004	0.005	0.018†
	o	0.001*	0.002*	0.003**	0.009
	po	-0.006§	¶	0.000	¶
100-seed weight, g	p	0.758**	0.004	0.041	0.290
	o	0.308**	0.169**	0.000	0.282
	po	0.385	¶	-0.013	¶
Pure live seed, %	p	14.955**	8.339*	23.457**	46.599
	o	0.568†	1.926	5.533	45.805
	po	6.275	¶	5.376	¶
1-year estimates					
IVDMD, %	p	2.503**	3.190+	-	-
	o	0.627*	2.378	-	-
	po	0.647	¶	-	-
Crude pro- tein, %	p	0.119*	0.347	-	-
	o	0.064**	0.145	-	-
	po	0.054	¶	-	-

†, *, ** Significant at the 0.10, 0.05, and 0.01 probability levels, respectively.

‡ No F-tests were possible for these variance components in this column.

§ Covariance between parents and HS offspring (po), no F-tests were possible.

¶ No estimate. Expected value is zero.

Genetic variance components due to: HS families and parents ($s^2_{G\#}$); HS families (or parents) by year interaction (s^2_{GY}); main unit error (s^2_m); among and within plot experimental error (s^2_e and s^2_w), respectively.

Table 4. Narrow-sense heritability estimates on a mean and individual plant basis for selected agronomic characters in eastern gamagrass.

Character	H_f^\dagger	H_i	H_{po}
	----- % -----		
Plant weight, kg	21 ± 20	5 ± 10	0 ± 21
100-seed weight, g	80 ± 7	66 ± 18	94 ± 21
Pure live seed, %	6 ± 40	1 ± 9	36 ± 20
IVDMD, %	51 ± 16	36 ± 23	39 ± 23
Crude protein, %	64 ± 18	39 ± 21	52 ± 14

† Narrow-sense heritability on a HS family basis (H_f), individual plant basis (H_i), and using parent-offspring regression of plot means (H_{po}).

Table 5. Expected genetic gains for selected agronomic characters in eastern gamma-grass from one cycle of individual plant (G_i), half-sib family (G_f), and progeny test (G_p) selection.

Character	G_i	G_f	G_p
	----- % of mean -----		
Plant weight, kg	1.3	1.3	+
100-seed weight, g	9.9	5.4	12.3
Seed emergence, %	0.4	0.6	8.5
IVDMD, %	1.5	0.9	1.5
Crude protein, %	3.0	2.0	3.0

† The covariance between parents and offspring was negative and H_{po} was set to zero.

CHAPTER III

INBREEDING EFFECTS FOR SELECTED AGRONOMIC CHARACTERS IN EASTERN GAMAGRASS

Abstract

A 2-year field experiment was conducted to determine the effects of inbreeding in eastern gamagrass (*Tripsacum dactyloides* L.) for plant height (PH), plant weight (PW), 100-seed weight (SW), and fertility measured by the percent of florets containing pure live seed (PLS). The material investigated included 20 eastern gamagrass lines each consisting of parental clones and their S_1 and S_2 generations. The parents were randomly selected offspring from a random mating composite population tracing to germplasm collected from throughout the southern Great Plains. Each parent was selfed to produce the S_1 offspring, and S_2 offspring were obtained by selfing a randomly selected S_1 from each of the 20 lines. Twenty ramets of each parent, 822 S_1 seedlings, and 593 S_2 seedlings were planted in the field in a completely randomized design.

Several S_1 and S_2 plants did not survive the experiment because of reduced vitality. During the spring, the foliage of some S_1 and S_2 plants was yellow; but it assumed a darker green color by summer. Two S_1 plants from the same line

produced inflorescences with female florets only. A number of albino plants were noted among the open-pollinated seedlings of parent and S_1 plants. Significant variation was present for all plant and seed characters during both years of the study. Significant line by year and generation within line by year interactions were detected for PLS. There was a significant decrease in PH, PW, and SW between the parents and the S_1 generation; but there were no consistent differences between the S_1 and S_2 generations. More than two-thirds of the parents had significantly higher values than their respective S_1 and S_2 generations for PH and PW. None of the comparisons between generations within lines were significant for SW in 1982; but in 1983, three-fourths of the parents had significantly greater SW than their S_1 or S_2 generation progenies. Less than half of the parents had greater PLS percentages than their corresponding S_1 and S_2 generation progenies in 1982, and there were even fewer differences in 1983.

Additional index words: Tripsacum dactyloides L., Inbreeding depression, Gene mutations, Male sterility, Plant height, Plant weight, Seed weight, Pure live seed.

Introduction

Eastern gamagrass (*Tripsacum dactyloides* L.) is a perennial, warm-season, tall-growing bunchgrass native to the eastern USA. The species is protogynous and normally cross-fertilized, but can be easily self-fertilized. It is related to maize (*Zea mays* L.) and the two species have been crossed extensively to study their cytotaxonomic relationships. Work by Galinat (4) and de Wet and Harlan (3) indicated that several loci are common to the maize and gamagrass genomes. Field studies by de Wet and Harlan (3) and Harlan and de Wet (5) demonstrated that maize-gamagrass introgression was possible, but that the probability of natural introgression was "infinitesimally small".

Eastern gamagrass has not been used extensively as a forage because of inadequate seed production, inferior seed quality, difficulties in vegetative establishment, and lack of persistence under grazing (1, 7). The species is adapted primarily to alluvial soils and would probably need an environment of this type to grow vigorously. For the species to be accepted by forage producers, yield, quality, and persistence must be competitive with other crops adapted to similar sites. Wright et al. (8) reported that significant variation existed among 51 gamagrass accessions (collected from throughout Oklahoma and Texas) for each of several agronomic characters they studied. Ahring and Frank (1) demonstrated that good stands of gamagrass could be established if high quality seed were sown in the winter.

Self-fertilization in normally cross-fertilized species usually results in inbreeding depression. Inbreeding exposes recessive alleles as homozygotes that would otherwise remain sheltered in heterozygotes. Those recessives thereby are exposed to natural or artificial selection, and a reduction in "fitness" of inbred lines generally results (2).

I am aware of no published data on the effects of inbreeding in eastern gamagrass. Information of this nature would be useful in the development of a breeding program to avoid the effects of inbreeding, if it exists, or to utilize selfing as a method to remove deleterious alleles from the population. This study was undertaken to determine the effects of inbreeding under complete self-fertilization on plant height, plant weight, 100-seed weight, and fertility of eastern gamagrass.

Materials and Methods

A 2-year study was conducted on the Agronomy Research Station, Stillwater, Okla., and included clonal propagules of 20 parental plants and their respective S_1 and S_2 offspring. The 20 parents were randomly selected from a space-planted nursery of open-pollinated plants from a highly heterogeneous, heterozygous population originating from a composite of germplasm collected from throughout Kansas, Oklahoma, and Texas. The 20 parents were selfed by removing the staminate portions of inflorescences prior to

anthesis and then placing pollination bags over the emasculated heads. Later, pollen was collected from intact inflorescences on the same plant by shaking the inflorescence within a pollination bag. The pollen was then placed on the stigmas of the emasculated heads. The selfed seed were harvested and bulked in separate lots for each of the 20 parents. The following year, a few S_1 seed from each parent were germinated and from among these, one S_1 seedling was randomly selected and planted in the field adjacent to the parental plant from which it was produced. The parents and S_1 plants were again selfed to produce S_1 and S_2 offspring.

During March 1981, selfed seed from the parental and S_1 plants were germinated in the greenhouse; and the seedlings planted into 10 X 10 cm paper pots. Twenty ramets of each parent plant were started in individual containers in the greenhouse at this time. The 400 parental clones, 822 S_1 , and 593 S_2 seedlings were space-planted into the field at 3.6 m centers in May 1981 (Table 1). A completely randomized design was used since differences among the lines in plant vigor and self-fertility resulted in unequal numbers of S_1 and S_2 progeny within lines. In early March 1982 and 1983, the study was burned and the Kirkland silt loam soil (Abruptic Paluustoll) was fertilized with 80 kg N/ha. A preemergent herbicide was applied March 1983 to help control weeds.

During July 1982, 15 to 20 open-pollinated seed heads

were harvested from each plant. Seed was air dried and then threshed by hand. A total of 50 seed from each harvested sample were weighed in g. The 50-seed weight was doubled to attain the 100-seed weight value (SW) used in the data analysis. Percent seedling emergence was used as an estimate of basic plant fertility expressed as percentage of florets containing a pure live seed (PLS). During November 1982, PLS was determined by planting the 50 seed into flats filled with vermiculite. Each flat contained 10 rows with 50 seed/row. Seedling emergence began about 3 weeks after planting, and seedling counts were taken on 4 dates at 2 week intervals once emergence started. PLS percentages for seed collected in 1982 was much lower than expected, so seed head harvest in 1983 was delayed until August.

The height (PH) and weight (PW) was determined for each plant during August 1982 and 1983. The height of foliage for each plant was measured from ground level after it was tied at the center with binder cord. The bundled plants were then cut at a height of 20 cm with a small sickle bar mower. Each plant was weighed in the field, and this weight was not adjusted for moisture.

The data for PH, PW, SW, and PLS were analyzed for each year separately and then combined into analyses over years. Sources of variation included lines, generations within lines, and the experimental error for the single-year analyses. For the combined analyses the year, line by year, and generation within line by year interactions were

computed. Single degree of freedom comparisons among the parents and their S_1 and S_2 progeny were computed to substantiate trends observed among the generation means. The comparisons performed included the parent vs. S_1 offspring, parent vs. S_2 offspring, and S_1 vs. S_2 offspring.

Results and Discussion

Differential fertility (sterility) occurred for parent and S_1 plants selfed in the field (Table 1). Field notes taken at the end of September 1981 and at both harvest dates in August 1982 and 1983 indicated that several S_1 and S_2 offspring did not survive through the experiment because of reduced vitality. Most of these S_1 and S_2 plants (55 and 34, respectively) did not survive the summer months after being transplanted in May 1981.

Yellow spring growth was observed on several S_1 and S_2 plants in April of both years, but the foliage on those plants gradually became greener as the season progressed (Table 2). Yellow and albino plants were also found among the open-pollinated seedlings in the greenhouse seedling emergence tests. Further genetic studies have been planned to elucidate the inheritance of the yellow and albino foliage colors.

During June 1982, the plants in the study were inspected for the possible presence of male sterility. Two S_1 plants produced from the parent in line 18 displayed

female florets on the upper, as well as the lower, portion of the racemes. Male florets were absent from the entire inflorescence, and the number of stigmas extruded from each female floret was increased from two to four. This character should be valuable for increasing seed production and producing controlled crosses. However, the overall vigor of the two plants was reduced; and the long, curled racemes shattered very easily. This inflorescence trait will be transferred via backcrossing to other lines because it should prove to be a valuable asset in eastern gamagrass breeding programs.

Significant variation ($P \leq 0.01$) existed among lines and among generations within lines for all characters during both years of the study. Years were also a significant source of variation ($P \leq 0.01$) for all characters in the combined analyses. No significant line by year or generation within line by year interactions were detected for PH, PW, and SW; however, both sources of variation were significant ($P \leq 0.01$) for PLS. The significant interaction which occurred for PLS was expected because of the low values observed for this character in 1982 ($\bar{x} = 2.7$ and 29.7%, for 1982 and 1983, respectively). The ranges for PLS percentages were similar for parents and progeny within each year, but the highest values in 1983 were twice as large as the highest values in 1982 (Table 3). In 1982, seed was harvested in July, a month before the entire plant was harvested to determine PW. Seed shatter on some entries had

started by that time; but the seed heads were, for the most part, still intact. During 1983, seed heads were harvested at the same time PH and PW were determined, even though a large proportion of the seed had already shattered. The extra month of ripening for seed that remained resulted in a 10-fold increase in overall mean emergence percentage.

The data for the remaining characters were combined over years since the genotype by year interaction was not significant. Significant ($P \leq 0.01$) differences were observed among the parent, S_1 , and S_2 generation means for PH, PW, and SW (Table 3). The means for parental clones for these three characters were significantly greater ($P \leq 0.01$) than respective means for S_1 or S_2 generations, but the differences between the S_1 and S_2 generation means were not significant. A decrease of 8, 30, and 19% in PH, PW, and SW, respectively, occurred between the parent and S_1 generation. The percent decrease from the S_1 to the S_2 was 0, 1, and 2% for PH, PW, and SW, respectively.

The ranges for the parents and offspring for PH, PW, and SW were similar in magnitude (Table 3). The error coefficients of variation (CV) were lower for the parents than for the S_1 or S_2 generations, but they were of similar magnitude for the two progeny populations. This result was expected because parental plants were asexually propagated material (clones) while the S_1 and S_2 generations had been advanced sexually by seed. Variation among parental clones within a line was environmental while variation among S_1 and

S_2 plants within a line was environmental plus genetic.

In both years of the experiment, the trends for PH and PW were similar (i.e. the parental values were significantly greater than the values for S_1 or S_2 progeny in approximately two-thirds of the lines) (Table 4). The S_1 or S_2 progeny were not significantly greater than the parent for PH in a single instance. For PW the S_1 mean for line 10 was significantly greater ($P \leq 0.05$) than that of either the parental or S_2 generations. The decrease in SW attributable to selfing was not evident in 1982; but in 1983 significant ($P \leq 0.05$) differences were found between parents and their S_1 or S_2 generations in some three-fourths of the lines. Lines 4 and 6 in 1983 had S_2 generations with significantly higher means than their parents.

Comparisons of generation means within lines for PLS indicated no consistent detrimental effect due to selfing (Table 4). In 1982, comparisons of parental vs. S_1 or parental vs. S_2 means for PLS showed that parental means were significantly ($P \leq 0.05$) greater than those of their respective S_1 or S_2 progenies about half the time. In 1983, parental means were significantly ($P \leq 0.05$) greater than their corresponding S_1 or S_2 generation means in only three cases.

In summary, differences in self-fertility occurred among the lines. Inbreeding caused a decrease in PH, PW, and SW; but no apparent decrease in PLS. Yellow and albino plants increased as a consequence of the fact that inbreeding

reduces the number of heterozygous loci. Two S_1 plants that produce inflorescences with female florets only were also identified. These gamagrass plants will be useful for increasing seed production and producing controlled crosses.

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Table 1. Number of seedlings transplanted in 1981 and plants harvested in 1982 and 1983 for eastern gamagrass parental (P), S₁ and S₂ generations.

Line number	Seedlings transplanted, May 1981			Plants harvested					
				August 1982			August 1983		
	P	S ₁	S ₂	P	S ₁	S ₂	P	S ₁	S ₂
	----- no. -----								
1	20	19	6	20	19	6	20	19	6
2	20	56	24	20	44	20	20	42	20
3	20	38	19	20	36	19	20	35	19
4	20	8	28	20	8	28	20	8	28
5	20	47	3	20	47	3	20	47	3
6	20	58	10	20	51	8	20	51	8
7	20	35	20	20	34	19	20	34	19
8	20	42	17	20	37	11	20	35	11
9	20	41	23	20	38	23	20	38	23
10	20	8	23	20	8	21	20	8	21
11	20	28	25	19	26	23	19	24	23
12	20	133	28	20	131	28	20	131	28
13	20	25	41	20	25	37	20	25	36
14	20	25	7	20	21	7	20	19	7
15	20	39	10	20	33	7	20	33	7
16	20	43	129	19	42	128	19	41	127
17	20	32	26	19	30	26	19	29	26
18	20	62	48	19	57	41	19	57	40
19	20	27	37	17	27	38	17	27	38
20	20	56	69	20	53	66	20	53	66
Total	400	822	593	393	767	559	393	756	556

Table 2. Number of chlorophyll deficient plants in the field and in seedling emergence analyses for eastern gamagrass parental (P), S_1 , and S_2 generations.

Line number†	Yellow plants in the field‡		Abnormal seedlings in emergence analyses				
			Yellow			Albino§	
	S_1	S_2	P	S_1	S_2	P	S_1
			no.				
2	0	0	0	5	1	0	0
3	1	0	15	18	1	11	0
4	1	0	0	0	0	0	0
6	0	0	1	2	0	0	0
7	0	0	0	2	1	0	0
10	0	0	0	0	0	3	0
11	1	1	0	0	0	1	3
12	0	0	0	4	0	0	0
13	0	2	3	3	0	0	0
15	2	0	0	0	0	0	1
16	11	21	3	0	2	0	0
17	0	0	0	0	0	0	1
18	0	1	0	0	0	0	0
19	0	1	0	0	0	0	0
20	0	0	0	2	0	0	0
Total	16	26	22	36	5	15	5

† Lines 1, 5, 8, 9, and 14 exhibited no chlorophyll deficient plants.

‡ None of the parental clones were chlorophyll deficient plants.

§ None of the S_2 seedlings exhibited chlorophyll deficient plants.

Table 3. Means, ranges, and coefficients of variation for selected agronomic characters for eastern gamagrass parental, S_1 , and S_2 generations.

Character	Gener- ation	Mean \pm SE†	Range	Error CV‡
2-year estimates				
Plant height, m	P	1.3 \pm 0.01	0.8 - 1.7	9.5
	S_1	1.2 \pm 0.01	0.5 - 1.7	13.3
	S_2	1.2 \pm 0.01	0.4 - 1.6	13.0
Plant weight, kg	P	1.9 \pm 0.02	0.05 - 3.8	31.0
	S_1	1.5 \pm 0.02	0.05 - 4.2	44.6
	S_2	1.5 \pm 0.02	0.05 - 4.1	43.5
100-seed weight, g	P	7.7 \pm 0.06	2.50 - 12.04	20.0
	S_1	6.5 \pm 0.04	2.00 - 12.32	25.3
	S_2	6.4 \pm 0.06	0.85 - 14.06	27.1
1-year estimates				
<u>July 1982</u>				
Pure live seed, %	P	2.9 \pm 0.3	0.0 - 38	183.2
	S_1	2.5 \pm 0.2	0.0 - 38	200.3
	S_2	2.8 \pm 0.2	0.0 - 42	189.9
<u>Aug 1983</u>				
Pure live seed, %	P	31 \pm 0.9	0.0 - 80	57.5
	S_1	28 \pm 0.6	0.0 - 90	61.8
	S_2	28 \pm 0.8	0.0 - 88	62.0

† Standard error of the mean.

‡ Coefficient of variation, %.

Table 4. Summary of single degree of freedom comparisons for selected agronomic characters for eastern gamagrass parental (P), S_1 , and S_2 generations.

Character	P vs S_1 †		P vs S_2 †		S_1 vs S_2 ‡	
	1982	1983	1982	1983	1982	1983
Plant height, m	13:0	16:0	13:0	12:0	5:5	3:0
Plant weight, kg	14:1	17:1	13:0	14:0	6:5	2:1
100-seed weight, g	0:0	16:0	0:0	16:2	0:0	9:6
Pure live seed, %	7:8	3:0	8:7	3:1	7:7	1:1

† Ratio of significant ($P \leq 0.05$) differences where the parental mean was greater than its corresponding S_1 or S_2 generation to differences where the S_1 or S_2 mean was greater than its parent.

‡ Ratio of significant ($P \leq 0.05$) differences where the S_1 mean was greater than the S_2 to differences where the S_2 mean was greater than the S_1 .

APPENDIX A

The tables in this appendix were prepared to help select the outstanding parental clones, half-sib (HS) families, or individual F_1 offspring. Since F_1 offspring were sampled at random each year (i.e., the same set of offspring were not necessarily sampled for each year) individual F_1 offspring were ranked by their respective replication deviations for the year sampled.

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Table A1. Ranked plant weight means averaged over replications, years, and plants within a plot for parents and half-sib (HS) families of eastern gamagrass.

Family	Plant weight	
	Parent	HS family
	----- kg -----	
24	1.05	0.84 (12)†
13	1.04	0.78 (25)
6	1.02	0.79 (22)
19	1.01	0.83 (14)
9	0.98	0.93 (3)
14	0.98	0.79 (22)
23	0.98	0.82 (16)
12	0.98	0.81 (19)
7	0.93	0.89 (8)
22	0.93	0.93 (3)
8	0.92	0.88 (10)
18	0.89	0.85 (11)
17	0.87	0.80 (20)
21	0.85	0.89 (8)
4	0.83	0.78 (25)
20	0.82	0.92 (5)
25	0.82	0.93 (3)
10	0.82	0.89 (8)
5	0.79	1.01 (1)
1	0.79	0.82 (16)
11	0.77	0.79 (22)
3	0.74	0.82 (16)
15	0.72	0.91 (6)
16	0.65	0.81 (19)
2	0.62	0.83 (14)
\bar{x}	0.87	0.85
LSD _{0.05}	0.08	0.04
CV‡	14.9	10.5

† Indicates rank of HS family mean.

‡ Coefficient of variation, %.

TABLE A2. Plant weights and deviations from their replication mean for the 20 highest and 20 lowest F_1 progeny sampled in 1982 and 1983.

Plant identification				Plant weight	
Year	Rep.	Male	Fem.	Rep. dev.	Observed value
20 Highest				-----	kg -----
1983	1	5	2	1.03	1.80
1983	2	3	2	1.00	1.56
1983	3	25	2	0.78	1.54
1982	2	15	1	0.69	1.73
1983	2	22	2	0.68	1.24
1983	1	25	1	0.58	1.35
1983	3	4	1	0.57	1.32
1982	2	19	2	0.56	1.61
1983	4	17	1	0.56	1.16
1983	3	20	1	0.55	1.30
1983	4	18	1	0.54	1.14
1982	1	10	1	0.52	1.51
1983	1	9	1	0.49	1.26
1982	3	24	2	0.48	1.53
1983	2	10	2	0.48	1.04
1983	1	14	1	0.47	1.23
1983	3	7	2	0.46	1.22
1982	1	5	2	0.46	1.45
1982	2	7	1	0.46	1.50
1983	3	10	2	0.45	1.21
20 Lowest					
1983	3	14	2	-0.45	0.30
1983	3	11	1	-0.46	0.30
1983	1	2	1	-0.46	0.30
1982	1	18	1	-0.48	0.51
1983	1	6	1	-0.49	0.28
1983	3	13	1	-0.49	0.27
1983	4	3	1	-0.49	0.12
1982	4	10	1	-0.49	0.55
1982	4	3	2	-0.52	0.53
1983	3	19	2	-0.52	0.23
1983	1	1	1	-0.56	0.21
1983	1	15	1	-0.56	0.20
1983	3	19	1	-0.57	0.19
1983	1	6	1	-0.58	0.19
1982	4	16	1	-0.61	0.44
1982	2	16	2	-0.65	0.40
1983	1	4	2	-0.66	0.11
1983	1	18	2	-0.66	0.10
1982	4	24	1	-0.69	0.35
1982	4	19	2	-0.97	0.07

Table A3. Ranked 100-seed weight means averaged over replications, years, and plants within a plot for parents and half-sib (HS) families of eastern gamagrass.

Family	100-seed weight	
	Parent	HS family
	g	
9	9.9	8.8 (3)†
11	9.3	8.6 (6)
20	9.3	9.1 (1)
25	9.2	8.7 (5)
17	9.1	7.9 (12)
15	8.8	8.1 (10)
21	8.6	8.9 (2)
19	8.5	8.4 (9)
13	8.4	7.7 (14)
1	8.3	8.7 (4)
7	8.2	7.4 (21)
10	8.2	7.2 (23)
16	8.2	8.4 (8)
12	8.1	7.9 (13)
3	7.9	7.6 (17)
22	7.8	8.5 (7)
18	7.6	7.1 (25)
8	7.5	7.4 (21)
24	7.5	7.9 (12)
23	7.2	7.5 (18)
14	7.1	7.3 (22)
2	6.9	7.4 (19)
6	6.8	7.6 (16)
5	6.7	7.1 (24)
4	6.6	7.6 (15)
\bar{x}	8.1	8.0
LSD _{0.05}	0.3	0.2
CV‡	6.7	6.6

† Indicates rank of HS family mean.

‡ Coefficient of variation, %.

TABLE A4. One hundred-seed weight and deviations from their replication mean for the 20 highest and lowest F_1 progeny sampled in 1982 and 1983.

Plant identification				100-seed weight	
Year	Rep.	Male	Fem.	Rep. dev.	Observed value
20 Highest				g	
1982	2	19	1	7.8	11.7
1982	2	9	2	6.9	10.8
1982	2	1	1	6.5	10.4
1982	2	11	2	6.3	10.2
1982	2	22	2	6.2	10.1
1982	2	1	2	6.0	9.9
1982	2	4	2	6.0	9.9
1982	2	1	2	6.0	9.9
1982	2	13	2	5.8	9.7
1982	2	16	2	5.7	9.6
1982	2	20	2	5.5	9.4
1982	2	4	2	5.4	9.3
1982	2	1	1	5.3	9.2
1982	2	21	2	5.2	9.1
1982	2	15	1	5.1	9.0
1982	2	16	2	5.1	9.0
1982	2	25	2	5.1	9.0
1982	2	25	1	5.0	8.9
1982	2	22	2	4.9	8.8
1982	2	3	2	4.9	8.8
20 Lowest					
1982	1	7	2	-2.1	5.6
1983	1	10	2	-2.1	5.8
1983	1	10	1	-2.1	5.7
1983	2	2	2	-2.2	6.0
1983	3	8	1	-2.2	5.9
1982	3	3	1	-2.2	5.6
1983	3	8	2	-2.2	5.9
1983	3	4	1	-2.3	5.7
1983	3	24	1	-2.4	5.7
1983	1	23	2	-2.4	5.4
1982	3	2	2	-2.5	5.3
1982	2	4	1	-2.6	5.5
1982	1	10	1	-2.8	4.9
1983	4	18	1	-2.9	5.2
1983	3	15	2	-3.0	5.1
1983	4	17	1	-3.0	5.1
1983	3	3	1	-3.0	5.0
1983	3	4	2	-3.5	4.6
1983	1	10	1	-3.7	4.1
1983	2	5	1	-3.7	4.4
1983	3	2	2	-3.8	4.3

Table A5. Ranked pure live seed means averaged over replications, years, and plants within a plot for parents and half-sib (HS) families of eastern gamagrass.

Family	Pure live seed	
	Parent	HS family
	-----	% -----
17	38.2	27.8 (11)†
16	35.8	27.5 (14)
9	35.0	30.1 (7)
20	33.7	31.0 (3)
3	33.1	22.1 (25)
12	33.0	32.8 (1)
25	32.9	27.5 (14)
7	32.7	30.3 (6)
24	32.0	27.6 (12)
5	31.9	26.9 (16)
1	31.1	27.8 (11)
6	30.2	27.1 (15)
18	28.6	26.2 (17)
22	27.7	29.2 (8)
2	27.0	25.6 (18)
11	26.3	32.3 (2)
4	26.1	28.6 (9)
8	24.1	25.0 (20)
23	23.7	22.4 (24)
15	23.6	24.7 (21)
14	23.4	22.5 (23)
13	23.1	25.4 (19)
19	21.6	30.5 (4)
21	21.2	30.4 (5)
10	16.7	22.7 (22)
\bar{x}	29.1	28.4
LSD _{0.05}	4.0	2.8
CV‡	23.5	24.1

† Indicates rank of HS family mean.

‡ Coefficient of variation, %.

Table A6. Percent pure live seed and deviations from their replication mean for the 20 highest and 20 lowest F_1 progeny sampled in 1982 and 1983.

Plant identification				Pure live seed	
Year	Rep.	Male	Fem.	Rep. dev.	Observed value
20 Highest				-----	% -----
1983	1	11	2	47.3	96.0
1983	3	22	2	47.2	96.0
1983	1	20	1	39.3	88.0
1983	3	4	2	39.2	88.0
1983	1	8	2	37.3	86.0
1983	3	11	2	35.2	84.0
1983	4	12	1	35.2	84.8
1983	1	21	1	33.3	82.0
1983	1	9	2	33.0	80.0
1983	1	4	2	31.3	80.0
1983	1	11	2	31.3	80.0
1983	2	7	2	31.2	80.0
1982	1	21	1	29.5	36.0
1983	2	16	2	29.3	78.0
1983	2	22	2	29.0	76.0
1983	4	8	2	28.4	78.0
1983	4	11	1	28.4	78.0
1983	3	11	1	27.2	76.0
1983	2	12	1	27.0	74.0
1982	3	2	1	27.0	34.0
20 Lowest					
1983	2	4	1	-27.0	20.0
1983	2	10	2	-27.0	20.0
1983	2	21	2	-27.0	20.0
1983	1	15	2	-28.7	20.0
1983	3	25	1	-28.8	20.0
1983	2	1	1	-29.0	18.0
1983	2	8	2	-29.0	18.0
1983	4	2	2	-29.6	20.0
1983	4	17	1	-29.6	20.0
1983	3	15	2	-32.1	16.7
1983	1	3	2	-32.7	16.0
1983	1	10	1	-32.7	16.0
1983	4	23	1	-33.6	16.0
1983	3	8	1	-34.8	14.0
1983	3	16	2	-34.8	14.0
1983	3	21	2	-34.8	14.0
1983	3	21	2	-34.8	14.0
1983	1	22	1	-36.7	12.0
1983	1	25	1	-38.7	10.0
1983	3	2	2	-44.1	4.7

Table A7. Ranked in vitro dry matter disappearance (IVDMD) means averaged over replications, years, and plants within a plot for parents and half-sib (HS) families of eastern gamagrass.

Family	IVDMD		
	Parent	HS family	
	%		
16	61.9	58.4	(1) †
2	58.1	56.4	(17)
19	57.8	57.4	(5)
6	57.7	54.6	(24)
14	57.0	55.9	(20)
13	56.9	58.1	(3)
23	56.7	57.1	(9)
10	56.6	57.0	(10)
24	56.6	56.6	(13)
11	56.5	56.5	(15)
18	56.4	56.6	(13)
21	56.3	55.7	(21)
4	56.3	56.9	(11)
17	56.2	56.4	(17)
25	56.1	57.2	(7)
20	56.0	58.2	(2)
3	55.7	57.2	(7)
22	55.7	56.0	(19)
15	55.3	54.9	(22)
1	55.2	54.3	(25)
12	54.8	57.8	(4)
8	54.7	57.2	(7)
5	53.8	56.2	(18)
9	53.7	54.7	(23)
7	51.9	56.6	(13)
\bar{x}	56.2	56.6	
LSD _{0.05}	1.5	0.9	
CV‡	2.8	1.4	

† Indicates rank of HS family mean.

‡ Coefficient of variation, %.

TABLE A8. Percent in vitro dry matter disappearance (IVDMD) and deviations from their replication mean for the 20 highest and 20 lowest F_1 progeny sampled in 1982.

Plant identification				IVDMD	
Year	Rep.	Male	Fem.	Rep dev.	Observed value
20 Highest				-----	% -----
1982	1	20	2	6.0	66.0
1982	2	13	2	6.0	61.0
1982	1	20	2	6.0	66.0
1982	4	9	1	6.0	62.0
1982	2	10	2	6.0	61.0
1982	4	25	2	6.0	62.0
1982	1	6	2	6.0	66.0
1982	3	16	2	5.0	61.0
1982	4	2	2	5.0	61.0
1982	2	17	1	5.0	60.0
1982	4	15	2	5.0	61.0
1982	1	13	1	5.0	64.0
1982	1	16	1	5.0	64.0
1982	3	8	2	5.0	60.0
1982	3	20	2	4.0	60.0
1982	2	3	2	4.0	59.0
1982	2	3	2	4.0	59.0
1982	4	13	1	4.0	60.0
1982	3	16	1	4.0	60.0
1982	1	12	1	4.0	64.0
20 Lowest					
1982	4	22	2	-4.0	52.0
1982	1	9	1	-4.0	55.0
1982	1	15	1	-5.0	55.0
1982	2	6	1	-5.0	50.0
1982	3	6	1	-5.0	51.0
1982	4	1	1	-5.0	51.0
1982	4	14	2	-5.0	51.0
1982	1	14	1	-5.0	55.0
1982	2	6	2	-5.0	50.0
1982	1	9	2	-5.0	55.0
1982	2	3	1	-5.0	50.0
1982	4	5	1	-5.0	51.0
1982	1	9	2	-5.0	54.0
1982	3	15	1	-6.0	50.0
1982	4	6	1	-7.0	49.0
1982	3	1	2	-7.0	48.0
1982	2	1	2	-8.0	47.0
1982	1	2	1	-8.0	52.0
1982	4	15	1	-9.0	47.0
1982	1	9	1	-12.0	47.0

Table A9. Ranked percent crude protein means averaged over replications, years, and plants within a plot for parents and half-sib (HS) families of eastern gamagrass.

Family	Crude protein	
	Parent	HS family
	----- % -----	
2	9.9	9.6 (1) †
14	9.8	9.0 (11)
25	9.6	9.4 (4)
19	9.5	9.2 (7)
22	9.5	8.8 (20)
8	9.4	9.2 (7)
1	9.4	8.7 (23)
4	9.3	9.4 (4)
20	9.2	9.0 (11)
10	9.2	9.2 (7)
23	9.2	8.9 (16)
17	9.2	8.9 (16)
9	9.1	8.8 (20)
16	9.0	9.4 (4)
15	9.0	8.8 (20)
21	8.9	9.0 (11)
7	8.9	9.5 (2)
6	8.9	8.1 (25)
12	8.9	8.8 (20)
11	8.7	8.7 (23)
5	8.6	8.9 (16)
18	8.6	8.9 (16)
24	8.4	9.0 (11)
13	8.2	9.0 (11)
3	8.2	8.7 (23)
\bar{x}	9.1	0.2
LSD _{0.05}	0.5	0.2
CV‡	6.5	4.2

† Indicates rank of HS family mean.

‡ Coefficient of variation, %.

TABLE A10. Percent crude protein and deviations from their replication mean for the 20 highest and 20 lowest F_1 progeny sampled in 1982.

Plant identification				Crude protein	
Year	Rep.	Male	Fem.	Rep. dev.	Observed value
20 Highest				-----	% -----
1982	4	18	2	3.2	12.2
1982	3	21	2	2.2	11.0
1982	1	4	2	1.9	11.2
1982	4	24	1	1.9	10.8
1982	3	10	2	1.9	10.6
1982	1	23	2	1.7	11.0
1982	3	2	1	1.7	10.5
1982	4	7	2	1.7	10.7
1982	2	9	2	1.6	10.5
1982	4	2	1	1.6	10.5
1982	1	14	2	1.5	10.8
1982	2	3	2	1.4	10.4
1982	4	3	2	1.4	10.4
1982	3	2	2	1.4	10.2
1982	3	19	1	1.4	10.2
1982	1	2	2	1.4	10.7
1982	1	7	2	1.4	10.7
1982	2	17	1	1.4	10.3
1982	2	7	2	1.3	10.3
1982	3	21	2	1.3	10.1
20 Lowest					
1982	3	17	2	-1.2	7.6
1982	2	1	2	-1.3	7.7
1982	3	6	2	-1.3	7.5
1982	4	6	1	-1.3	7.7
1982	1	6	1	-1.3	8.0
1982	2	3	1	-1.4	7.6
1982	4	10	2	-1.4	7.6
1982	2	6	2	-1.4	7.5
1982	4	22	2	-1.5	7.5
1982	3	18	2	-1.5	7.3
1982	2	6	1	-1.6	7.3
1982	1	9	1	-1.7	7.6
1982	4	6	2	-1.7	7.3
1982	4	5	1	-1.7	7.3
1982	3	6	1	-1.7	7.1
1982	3	9	1	-1.8	7.0
1982	4	3	2	-1.8	7.2
1982	2	18	1	-1.8	7.2
1982	1	15	1	-1.9	7.4
1982	1	3	2	-1.9	7.4

APPENDIX B

The tables in this appendix were prepared to help interpret the effect of inbreeding on plant height, plant weight, 100-seed weight, and percent seed emergence.

List of Tables

- Table B1. Plant height means for parental (P), S_1 , and S_2 generations for 1982 and 1983.
- Table B2. Plant weight means for parental (P), S_1 , and S_2 generations for 1982 and 1983.
- Table B3. One-hundred seed weight means for parental (P), S_1 , and S_2 generations for 1982 and 1983.
- Table B4. Pure live seed means for parental (P), S_1 , and S_2 generations for 1982 and 1983.

Table B1. Plant height means for parental (P),
 S_1 , and S_2 generations for 1982
 and 1983.²

Line	Year	P	S_1	S_2
----- m -----				
1	1982	1.47	1.34	1.17
1	1983	1.36	1.22	1.18
2	1982	1.30	1.20	1.19
2	1983	1.31	1.21	1.22
3	1982	1.32	1.28	1.13
3	1983	1.31	1.22	1.15
4	1982	1.23	1.20	1.23
4	1983	1.22	1.23	1.22
5	1982	1.28	1.15	1.03
5	1983	1.33	1.16	1.12
6	1982	1.39	1.23	1.32
6	1983	1.36	1.22	1.31
7	1982	1.21	1.13	1.15
7	1983	1.17	1.09	1.11
8	1982	1.34	1.22	1.07
8	1983	1.32	1.20	1.12
9	1982	1.22	1.08	1.21
9	1983	1.22	1.09	1.20
10	1982	1.36	1.37	1.28
10	1983	1.33	1.30	1.24
11	1982	1.37	1.20	1.14
11	1983	1.26	1.15	1.15
12	1982	1.26	1.26	1.25
12	1983	1.25	1.22	1.23
13	1982	1.40	1.30	1.27
13	1983	1.37	1.25	1.34
14	1982	1.30	1.16	1.13
14	1983	1.27	1.18	1.21

Table B1. (Continued.)

Line	Year	P	S ₁	S ₂
----- m -----				
15	1982	1.42	1.33	1.21
15	1983	1.39	1.28	1.18
16	1982	1.28	1.20	1.19
16	1983	1.27	1.19	1.19
17	1982	1.32	1.08	1.23
17	1983	1.31	1.10	1.23
18	1982	1.50	1.25	1.30
18	1983	1.47	1.25	1.24
19	1982	1.14	1.19	1.21
19	1983	1.16	1.19	1.25
20	1982	1.30	1.17	1.19
20	1983	1.30	1.16	1.15
	\bar{x}	1.3	1.2	1.2
	SD†	0.1	0.2	0.2
	CV‡	9.5	13.3	13.0

† Standard deviation of the mean.

‡ Coefficient of variation, %

Table B2. Plant weight means for parental (P), S_1 , and S_2 generations for 1982 and 1983.

Line	Year	kg		
		P	S_1	S_2
1	1982	2.27	1.74	0.90
1	1983	2.46	1.57	1.50
2	1982	1.47	1.13	1.33
2	1983	1.73	1.41	1.40
3	1982	1.95	1.74	1.08
3	1983	2.35	1.85	1.26
4	1982	1.54	1.39	1.04
4	1983	1.99	1.44	1.23
5	1982	1.81	1.25	1.25
5	1983	1.89	1.29	1.03
6	1982	2.45	1.72	1.78
6	1983	2.37	1.69	1.95
7	1982	1.91	1.28	1.19
7	1983	1.86	1.31	1.32
8	1982	2.02	1.56	1.16
8	1983	2.16	1.56	1.33
9	1982	1.63	0.94	1.45
9	1983	1.92	1.14	1.66
10	1982	1.52	2.16	1.49
10	1983	1.47	2.03	1.62
11	1982	2.17	1.49	1.28
11	1983	2.31	1.64	1.36
12	1982	1.44	1.75	1.77
12	1983	1.81	1.85	2.00
13	1982	1.69	1.44	1.24
13	1983	1.88	1.48	1.48
14	1982	1.73	1.05	0.82
14	1983	1.89	1.28	1.24

Table B2. (Continued.)

Line	Year	P	S ₁	S ₂
----- kg -----				
15	1982	2.12	1.66	1.34
15	1983	2.26	1.58	1.42
16	1982	1.47	1.29	1.73
16	1983	2.16	1.49	1.64
17	1982	2.38	1.09	1.37
17	1983	2.43	1.18	1.62
18	1982	1.96	1.30	1.55
18	1983	2.17	1.47	1.66
19	1982	.95	1.29	1.26
19	1983	1.24	1.23	1.40
20	1982	1.78	1.33	1.33
20	1983	1.88	1.45	1.25
	\bar{x}	1.9	1.5	1.5
	SD†	0.59	0.70	0.62
	CV‡	31.0	44.6	43.5

† Standard deviation of the mean.

‡ Coefficient of variation, %.

Table B3. One-hundred seed weight means for parental (P), S_1 , and S_2 generations for 1982 and 1983.

Line	Year	P	S_1	S_2
----- g -----				
1	1982	9.2	8.0	8.2
1	1983	8.8	7.4	6.8
2	1982	10.0	8.8	7.4
2	1983	9.2	8.4	7.2
3	1982	9.6	8.0	6.0
3	1983	9.6	7.8	5.2
4	1982	5.6	6.4	6.4
4	1983	5.0	5.2	6.2
5	1982	7.2	5.4	4.4
5	1983	6.4	4.6	3.4
6	1982	6.8	6.0	6.8
6	1983	6.2	5.8	6.6
7	1982	7.2	6.2	6.2
7	1983	7.4	5.8	5.8
8	1982	6.8	5.8	6.4
8	1983	6.2	5.4	6.4
9	1982	6.4	6.2	6.6
9	1983	7.0	5.8	6.0
10	1982	8.4	6.6	7.8
10	1983	8.8	6.6	7.2
11	1982	7.2	6.0	6.0
11	1983	6.6	5.8	6.2
12	1982	6.8	6.0	7.0
12	1983	7.0	6.0	6.6
13	1982	8.6	7.8	7.0
13	1983	8.6	8.0	6.8
14	1982	8.8	7.4	5.2
14	1983	7.6	6.8	4.6

Table B3. (Continued.)

Line	Year	P	S ₁	S ₂
----- g -----				
15	1982	8.0	7.0	5.2
15	1983	7.2	6.0	5.2
16	1982	9.4	7.6	7.6
16	1983	9.4	7.4	6.8
17	1982	9.0	7.0	7.2
17	1983	8.4	6.8	7.4
18	1982	6.4	5.6	5.2
18	1983	6.2	5.4	4.8
19	1982	8.4	7.2	6.2
19	1983	7.8	7.0	6.0
20	1982	8.8	7.2	5.0
20	1983	7.8	6.8	4.6
	\bar{x}	7.7	6.5	6.4
	SD†	1.5	1.6	1.7
	CV‡	20.0	25.3	27.1

† Standard deviation of the mean.

‡ Coefficient of variation, %.

Table B4. Seed emergence means for parental (P), S_1 , and S_2 progeny for 1982 and 1983.

Line	Year	P	S_1	S_2
----- % -----				
1	1982	1.4	1.7	0.0
1	1983	38.0	31.0	20.0
2	1982	3.1	1.1	2.7
2	1983	26.0	28.0	28.0
3	1982	0.6	2.1	1.6
3	1983	34.0	30.0	28.0
4	1982	0.7	1.4	2.2
4	1983	13.0	20.0	37.0
5	1982	1.4	1.0	1.0
5	1983	32.0	21.0	8.1
6	1982	4.3	4.2	5.1
6	1983	37.0	35.0	40.0
7	1982	0.5	0.7	0.4
7	1983	32.0	26.0	29.0
8	1982	4.7	5.2	1.4
8	1983	42.0	31.0	36.0
9	1982	2.2	3.6	3.9
9	1983	42.0	34.0	34.0
10	1982	2.7	2.0	2.3
10	1983	37.0	31.0	29.0
11	1982	1.2	0.7	0.3
11	1983	21.0	24.0	18.0
12	1982	1.1	1.6	5.5
12	1983	22.0	21.0	21.0
13	1982	4.8	5.0	2.1
13	1983	31.0	35.0	38.0
14	1982	4.3	6.3	3.4
14	1983	37.0	34.0	35.0

Table B4. (Continued.)

Line	Year	P	S ₁	S ₂
----- % -----				
15	1982	8.0	2.1	1.7
15	1983	38.0	38.0	27.0
16	1982	6.9	3.1	4.1
16	1983	40.0	36.0	29.0
17	1982	2.7	1.0	3.6
17	1983	37.0	27.0	30.0
18	1982	0.5	1.4	1.8
18	1983	17.0	21.0	18.0
19	1982	2.2	2.4	2.2
19	1983	21.0	22.0	25.0
20	1982	4.1	5.5	2.5
20	1983	30.0	32.0	31.0

VITA ²

Michael Patrick Kenna

Candidate for the Degree of

Doctor of Philosophy

Thesis: HERITABILITY ESTIMATES AND INBREEDING
EFFECTS FOR SELECTED AGRONOMIC CHARACTERS IN
EASTERN GAMAGRASS, TRIPSACUM DACTYLOIDS L.

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